THE CAUSE OF THE PRODUCTION OF "DOWN" AND OTHER DOWN-LIKE STRUCTURES IN THE PLUMAGES OF BIRDS.

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A recent paper ('07) by Dr. Lynds Jones makes clear the morphological relations of "down" and definitive feathers. Jones' work, some experimental results already reported by the writer ('07, '08), together with some hitherto unpublished data bearing on the physiology of avian plumages, now enable us to make some fairly definite statements concerning the causes which lead to the production of "down." A number of observations and experiments on the relations which exist between the *rate of growth* and the *character of the feather structure produced* — pennaceous or plumulaceous — also suggest some interesting conclusions. It will be shown later that results from these various angles of approach center about a common point.

Jones' studies demonstrate positively that "the first down and its succeeding definitive feather are produced by one continuous growth, and therefore cannot be regarded as two distinct feathers. The first down is the plumulaceous tip of the first definitive feather" (p. 17).

This writer has however failed to homologize the modified region which connects the two parts of such a feather with anything already known; and, apparently he has not perceived the actual cause of this modification. To point out the homologies and state the cause of the various modifications found in the down; to show how the "down" and the plumulaceous proximal parts of pennaceous feathers are related to their rate of growth; and in connection with this latter point to put forward a general theory of the significance and relations of all plumulaceous and pennaceous feather structures, is the purpose of the present paper.

Homologies of the Modified Region of the Down.

Anyone who is familiar with the several forms of feather defects or fault-bars which have elsewhere been fully described by the

writer ('07, '08), will find that Jones' plates and description practically prove the existence of another variety of this same defect; in other words one may say that the modified region of the down — the "quill" — is a variety of defect which we have already recognized in other situations, but which here occurs in a very uniform way — at a point near the end of the feathers of the first plumage. The fact is, simply, that the defective region falls so close to the end of the feather that it does not include any of the shaft of the feather to which it belongs.

There can be, I think, no question as to this interpretation. The exact conditions met with in the defects or fault-bars already referred to are to be found in the modified region of the down: (1) In the modification or absence of barbules (Davies '89, Jones); (2) in the occasional fusion of the barbs (Klee '86, Davies, Jones); (3) in the diminished differentiation (Davies, Jones) and growth (Davies); (4) in a defective development between a more distal and a more proximal part of the same feather (Jones).

Now if the "quill region" of the down is the morphological equivalent of the fault-bars (which are often produced "normally" and which have been produced at will experimentally, at all levels in the definitive feather), we should expect to find that the two have the same or a similar cause. What is the evidence for such a common cause? What causes the production of "down"?

The Cause of the Modifications in the Down.

It has been established beyond question that the several types of fault-bars are produced by insufficient nutrition; even the variations produced in the available food-supply by the daily fluctuations in blood-pressure was shown to be able to leave its mark on feather structure (Riddle '07, '08). What now is the evidence that reduced or insufficient nutrition is the cause of the modification which occurs near the distal ends of the first feathers of birds.

The most highly modified region of the down, *i. e.*, the "quill" region, is produced in all cases so far as I am able to ascertain, after and soon after the hatching of the bird. There are the following reasons for a defective nutrition at that time:

1. The whole source of food-supply for the young bird is now changed. Heretofore, as an embryo it has formed its tissues from substances once assimilated by the mother-bird and stored by her within the egg, from which it extracts them by means of the *yolk-sac*, — a provisional appendage of the gut; henceforth it is subject to the vicissitudes of a much greater and very competitive world for its food-supply; and its *entire alimentary tract*, with its various appendages, new and untried as it all is, must now begin to work — and work properly and successfully — on the hodge-podge of digestibles and indigestibles which here begin their intermittent flow into it. If there is ever such a thing as a "critical period" in a bird's life, indeed it is here! We should have the strangest of miracles performed before our very eyes if this transformation and adjustment were to occur instantaneously and without interruption of any of the nutritive processes of the animal.

2. The skin of the bird is exposed to the chilling and evaporating effects of the air; this doubtless lessens the blood-supply to the integumentary structures. This chilling, moreover, is now of all times the most effective, for, the bird now has the least plumage to help it retain its heat; then, too, the heat radiating surface — the skin — is greater in proportion to the mass of the animal than it will ever be again, and therefore the heat loss at that time is greatest. It is, of course, true that such an organism tends to make good the greater heat loss by increased heat production; but this latter process means at the same time, a greater use and destruction of food at a time when, as stated above, the nutritive mechanism of the animal has not got into full swing.

We are, however, in possession of some direct evidence that a faulty nutrition is the cause of the production of the "down."

1. If a chick is kept continuously underfed from the time of hatching and while in its downy plumage, it will be found that almost all of the feathers (except primaries, secondaries, and a few others) can be kept in the "downy" condition and the bird can thus be made to wear its downy plumage for months (many kept four to five months).

The "quill" region is a part of the feather which "normally" *almost* refuses to grow; by reducing the food-supply during and

after its formation further growth may be absolutely inhibited or stopped. If, therefore, faulty nutrition can and does completely halt the growth at the proximal part of the quill, there is every reason to believe that the same cause *may* have acted as the check upon the growth at the distal and all intermediate parts of the quill; and since it has been shown that the structures pro-

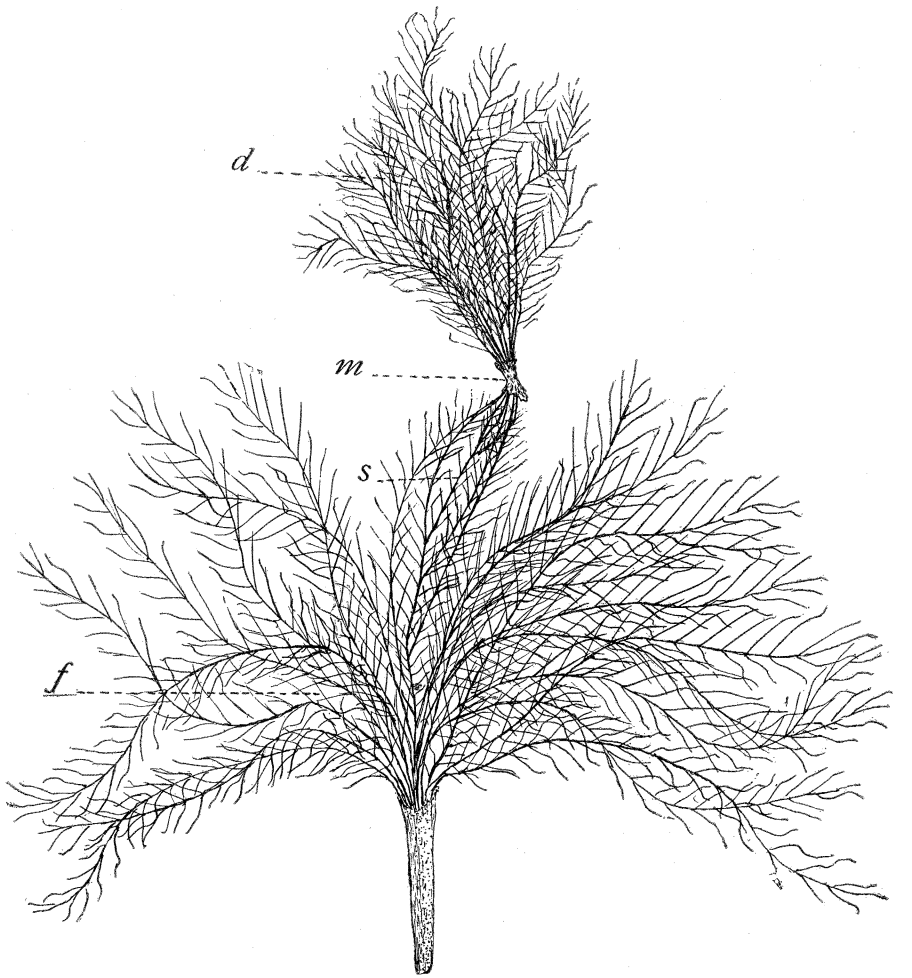

FIG. 1. A feather from the humeral tract of an underfed chick, four months old. *d*, downy portion; *m*, the highly modified basal region of the down, *i. e.*, the "quill." *s*, the barbule bearing shaft of the modified pennaceous feather *f* which grew under "starving" conditions and thus became downy or plumulaceous in character. Drawn with a camera lucida. Actual length of feather 3 cm.

duced in the "down-quill" are in every way similar to those of a series of defects known to be produced by malnutrition, it becomes extremely probable that an insufficient food-supply is he cause of the "quill" formation also.

2. The case just cited is supplemented and strengthened by the peculiar structure of certain feathers from the humeral region (of one of the chicks mentioned in the experiment above) which were able to continue their growth under the conditions of my experiment. These feathers have all the appearance and texture of down, excepting the presence of a very slender shaft. The barbs, however, are not closely set into this shaft as they are in a normally grown feather, but unite with it only at wide intervals. This is clearly an approximation to the conditions in the down where the barbs do not unite at all. The shaft, moreover, bears barbules and these again are exactly like those borne on barbs. Such a feather is shown in Fig. 1.

3. In the plumulaceous basal parts of the feathers of the chick I have produced structural conditions which are in many ways like those of down, and am in a position to state definitely that they were produced by "starving" the bird. In Fig. 2 is shown a section of a feather bearing such downy formations.

4. A fourth line of evidence that the down — or rather its basal portion — is produced under poor nutritive conditions is afforded by the fact that the most emphasized of the down malformations — the horny cylinder or quill — is to be found most frequently among the altricial birds as was pointed out by Jones. Jones does not state that the "quill" is the most extreme modification of these downy structures, but both his work and mine confirm that view.

I quote the following single paragraph which Jones writes on quill-formation, and which seems to include something else quite as important:

"The progress of transition which results in a so-called 'quill' or tube differs in some important particulars from that just given. In the early stages of development no difference is recognizable, but at a little later stage the whole mass of intermediate cells (Fig. 45, Pl. IV., *cl.in*) as well as the sheath cells (*cl.tu*) become much flattened, their nuclei elongated, and their

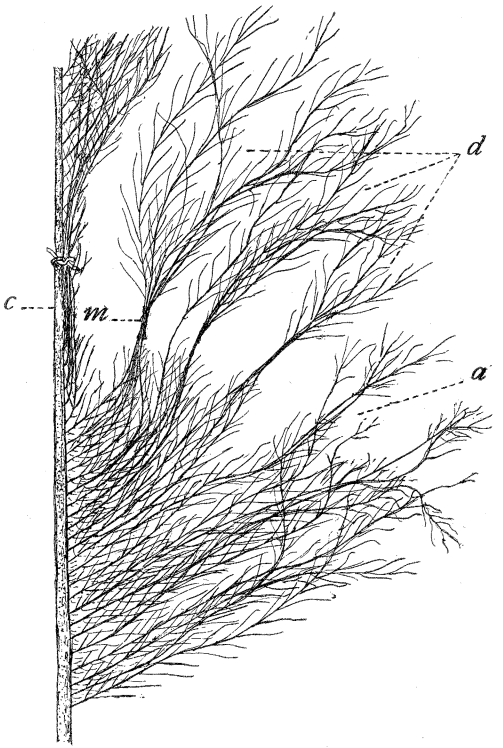

FIG. 2. A section of the proximal plumulaceous portion of a body covert from a chick, showing a modified region with "downy" formations *d*, the much-modified bases of which were produced during a "starving" period of two days. *m*, the horny covering (quill) of a bundle of six barbs; *a*, the abnormal area (fault-bar) produced at another point; *c*, the pigmentless part of the shaft which was grown during this period. Drawing made with camera lucida. Actual length of section shown 2 cm.

cell boundaries lost in a mass of fibrous tissue. Only the row of cells next to the pulp, representing the cylinder cell layer, retains its characteristic shape. At a still later stage in development, represented by Fig. 46, in which the epitrichial sheath is not shown, cornification of the outer rows of cells, representing the region of the sheath cells, has taken place, only suggestions of its original fibrous structure remaining. The outermost intermediate cells have become almost wholly fibrous, narrow spaces representing the position of the nuclei. The process of cornification now proceeds rapidly until practically all of the intermediate cells become cornified, and the cylinder cell layer becomes

fibrous. Fig. 33, Pl. III., represents the final stage in development. That the formation of this horny tube is wholly different from the process by which the shaft and quill of the definitive feather are formed, as described by Davies (p. 594 et seq.), is evident. Instead of being a process designed for the accomplishment of a definite work — the building of shaft and quill — it appears to be due to a lack of differentiation of the cell mass and a short cut to cornification of the tissues induced by a reduced blood supply to this part of the feather during the period when the cells would be showing differentiation if supplied with sufficient nourishment. It is significant that this condition of a cornified ring instead of the normal barb-vanes is more often found among the strictly altricial birds which are hatched in a helpless condition. It is well known that the first few days after the hatching of altricial birds are the most critical days of their lives. During this critical period there appears to be no growth of the down. An American robin which hatched on the fourteenth day of incubation possessed the usual down upon the head and back. These downs made no further growth. It was not until the fourth day after hatching that the skin gave evidence of the beginning of the definitive feathers. On the eighth day after hatching the skin surface was exposed to the drying influences of the air before renewed activity in the feather germ began. During this interval of four days the so-called 'quill' was formed at the proximal end of the down by the rapid drying of the imperfectly formed barb-vane ridges" (p. 13).

I wish to make a number of statements concerning the paragraph just quoted; for, from my point of view, a number of things are here touched — but hardly grasped — and, at any rate, not made really clear.

In the first place the statement is made (here and elsewhere) that in the formation of the "quill" a lack of *differentiation* is the process at fault. My own studies on similar structures — and I think Jones' plates, as well as some points of his description show the same — indicate that while lack of differentiation is undoubtedly a part of the process, a more important part is lack of *growth*. The barbules, for example, do not differentiate, but the cells which should form them do not *grow*. That is to

say, many of the necessary cells never arise at all and those which are to be found in the barbule region never attain the normal size of such cells. Davies recognized, to a certain extent at least, a deficiency of growth of particular parts of this region. He states, "Gewöhnlich verschwinden (in the quill) die Leisten nicht vollkommen, obgleich sie eine bedeutende verminderung ihre Grösse erfahren" (p. 581). On the other hand, one kind of differentiation, *i. e.*, cornification or development of keratin proceeds without interruption in all of these cases.

Jones further states that apparently this "lack of differentiation . . . is induced by a reduced blood supply to this part of the feather, etc." He is here speaking of the conditions in the "quill"-formations only and does not apply this statement to the other form of down modification which he considers (p. 11) the typical one. He does not furnish any evidence for the statement just quoted, and does not refer to the direct and conclusive evidence which my paper ('07) supplies — and I may add that this is still the only direct evidence we have — that a reduced blood supply tends to produce just such feather modifications as are represented in the quill of the down.

Jones' observation that there appears to be no growth of the down in altricial birds during "this critical period" is important and suggestive as supporting the view that wherever we find the "down" we can assert that it signifies defective nutritive conditions in the bird at the time that part of the feather was grown. It is, however, doubtful whether Jones had anything similar to this in mind, for it will be seen that his last word on this subject is that "in the robin (the only specific case cited) the so-called 'quill' was formed at the proximal end of the down by the *rapid drying* of the imperfectly formed barb-vane ridges."

Finally, it should be noted that Jones states that in the case of the young robins the "quill" was formed *during* the fourth to the eighth days after hatching. It seems to me extremely probable that the first four days after hatching were even more important in producing the modification than the four succeeding ones.

Rate of Growth in Relation to the Kind of Feather Structure Produced.

It is well known that "down"—*i. e.*, the distal plumulaceous tip of the feather—and the plumulaceous proximal parts of pennaceous feathers are similar as regards their appearance and texture. They all possess long, slender barbules—usually without hooked barbicles. So far as my observation goes all have the barbules set rather widely apart, and have a fluffy appearance. Since Jones has shown that the "down is the plumulaceous tip of the first definitive feather"; and since in all typical pennaceous feathers we have also a plumulaceous proximal end of the feather, what does it mean in the development of the first feather that two plumulaceous regions are produced with a pennaceous region between?

The writer is convinced that the type of feather structure produced is somehow quite definitely correlated with the relative *rate of growth* at which the various parts of the feather are developed. The following facts and observations are submitted in favor of this view:

1. That the "down" is of slow growth is proved by the works of several writers—Studer '73, Klee '86, Davies and Jones among others—who have shown that in various birds the down begins to develop from the fifth to the eighth day (in the egg) and continues usually fifteen to twenty days, or longer. This, when compared with the growth which succeeds it is obviously very slow. Dwight ('00) also notes that "during the early days of the newly-hatched chick (passerine birds) feather growth is comparatively slow, but shortly it proceeds with marvelous rapidity" (p. 99).

2. If a feather from a juvenal plumage is taken for consideration, it may be said that that part of the feather which lies between the "down" (plumulaceous) and the basal plumulaceous portion of the feather, is grown (rectrices or remiges of ring-dove) at an average of more than twice the rate of either of these extremities.

The slow rate of growth of "down" is self-evident. The following measurements in mm. of a rectrix of the ring-dove are given to show that the above statement is true as applied to the proximal plumulaceous growth.

TABLE I.

SHOWING RATE OF GROWTH OF RECTRIX OF RING-DOVE (*Turtur risorius*).

Days after appearance beyond skin.	1–4	5–8	9–11	12–15	16–20	21–25	26	27	28–32
Length of feather.	22	44	59	78	96	112	115	117	123
Average daily growth.	$5\frac{1}{2}$	$5\frac{1}{2}$	5	$4\frac{4}{5}$	$4\frac{1}{2}$ *	$3\frac{3}{5}$	3	2	$1\frac{1}{6}$

At the point indicated with the star (*), *i. e.*, at about 95 mm. from the distal tip of this feather, it is found that the plumulaceous formation begins. At first only those barbs which lie in the germ opposite to the shaft are affected; but as growth proceeds — and as the *rate of growth diminishes* — more and more barbs become affected.

After having watched the rate of growth of many feathers in chicks and doves only to find that the plumulaceous part always begins at the point of, or after, a considerable falling off in this rate of growth, one is tempted to the conclusion that in these feathers *the two kinds of feather growth, plumulaceous and pennaceous, are merely expressions of slow and rapid growth respectively.*

It is, I think, moreover, quite certain that for many birds the general rule can be laid down that those feathers which as a whole grow slowest have the greatest proportion of plumulaceous growth.

One is led by such considerations to inquire whether all strictly plumulaceous feathers are of slow growth. I know but little of these conditions from personal observation, but the known facts, in so far as I have been able to ascertain them, are in harmony with this view.

It is stated that the ostrich plumes grow at the rate of one inch per week. For such feathers of such birds this is indeed a slow rate — only about 3.5 mm. per day; whereas a little, newly hatched ring-dove will grow remiges and rectrices at from 5 to 7 mm. per day. I feel confident that it will be found that all plumulaceous feathers are grown at a relatively slow rate.

The aftershaft (hyporhachis) which is found in many feathers is another plumulaceous formation and like the others is of slow growth. It seems to me highly probable that a closer study of

the nutritive conditions in this region of feather-germs would reveal the reason for the presence of this feather-accessory in some plumes and its absence in others.

The true quill (calamus) also shares this slow growth of the proximal end of the feather. Indeed it is in the quill that we find the slowest rate of growth to be met with in the whole length of the feather. I am inclined to "explain" the quill as the type of feather formation which results from nutritive conditions which become slowly and progressively poorer; this in turn is able to almost completely stop growth and cell-division, but affects the process of cornification, *i. e.*, keratin formation, to a much smaller extent. It seems to me, too, that our knowledge of feather-growth (quill-formation) in the Japanese fowls, particularly the results of Cunningham's ('03) experiments, and many other facts support this conclusion. Neither the position nor the presence of a quill is "predetermined" in the feather, but both of these are merely marks left along the course of the ebbing tide of a greatly diminished feather nutrition.

The fact that plumulaceous structures do not show the maximum of growth and differentiation (*e. g.*, weaker barbs, and barbules without hooklets) together with the observation that such regions occasionally result from under-feeding (Fig. 1), would seem to lend weight to the view that such regions or such entire feathers are grown under nutritive conditions considerably below the optimum.

It should be remarked that if the view here put forward is correct it would lead us to expect a pretty general occurrence of growth-marks on all feathers which are growing at the time of hatching and soon thereafter. Such marks seem not to have been reported for the rather extraordinary first feathers of the Anserine birds. My own observations on this plumage of these birds are too meager to mention, but it seems quite probable that such marks are much less in evidence there — if they exist at a l — than in most other birds. It is conceivable, however, that the young of these birds have a greater quantity of egg-yolk left for their first day or two after hatching; or that they have a considerable store of available fat in their bodies; or yet another means of tiding them over the "critical period" which in these

birds is of course very short. On this point, however, I can furnish no observations of value, and can only say that the exact conditions in these forms are not clear.

It must be left to the further investigations of those who in the course of their studies are able to examine the plumages (particularly the plumulaceous ones) of all of the families of birds to decide whether the theory here advanced of the slow rate of growth of the several plumulaceous formations can be universally and absolutely applied. It is the hope of the writer that some one may have the material and the inclination to put this part of the work here reported to a more rigorous test than the writer's limited material has permitted him to do.

Methods and Materials.

For the experimental part of the work here reported only a few forms have been used; but these few animals have been very closely watched and studied. Nearly all the starving experiments were made on the young of the chick (*Gallus domesticus*), and both on the young and old of the ring-doves (*Turtur risorius*). For the modifications of the nature of the feather growth the chicks are by far the better material. Control experiments were maintained throughout.

It should be said that the under-feeding or "starving" of these animals was usually either accompanied or accomplished by the feeding of the fat-stain Sudan III., which appears to "tie up" the fats of the body. The stain was fed for a purpose not immediately connected with the results reported here, but there is little doubt that it has no specific action on the feathers except in so far as it helps to bring about "starving" conditions in the animal.

Summary.

1. The highly modified region of the "down" is in all respects similar to other feather defects or fault-bars which have already been described as occurring at any and all levels in definitive feathers.

2. Juvenal feathers can by under-feeding be made to persist (chick) in the "downy" conditions practically without growth for several months if the reduced feeding be begun immediately after hatching.

3. Occasionally feathers may be found which have been able to continue their growth proximal to the downy portion despite the inhibitory influences of the lack of food; such feathers have been found to represent a type of structure intermediate to the downy and pennaceous formations.

4. The cause of the modification at the base of the down is to be traced to an interruption, or at any rate to the inadequacy of the nutritive processes of the bird. This interruption is doubtless partly accounted for by the change of source of food from the embryonic to the adult life.

5. The apparent absence of such growth-marks in the feathers of the duck and other anserine birds remains unexplained.

6. The rate of growth of the two ends of a juvenal, pennaceous feather, and of the proximal ends of all pennaceous feathers which bear a plumulaceous proximal portion, is much slower than the rate of growth in the central pennaceous part of the feather.

7. It seems probable that all plumulaceous structures are produced at a relatively slow rate of growth; and also probable that during their growth they have not enjoyed optimum nutritive conditions.

8. The formation of the quill is probably the direct result of a progressive diminution of an already lessened food-supply.

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